Journal of Pharmacognosy and Phytochemistry

Available online at www.phytojournal.com

E-ISSN: 2278-4136
P-ISSN: 2349-8234
JPP 2018; 7(3): 2506-2510
Received: 03-03-2018
Accepted: 04-04-2018

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Gene action in interspecific crosses of tomato for fruit yield and important characters (*Solanum* section *lycopersicum*)

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Abstract
Tomato is a pulpy nutritious vegetable of solanaceae family grown throughout the world. The nature of gene action in the inheritance of yield per plant and some was studied deploying generation mean analysis following 6 parameter models for parents, F_1, F_2, B_1 and B_2 generations of five interspecific crosses of tomato. The scaling tests indicated the presence of epistasis for all the characters in different crosses except plant height in family I, number of primary branches per plant in family I and family III, number of fruits per plant in family V, fruit yield per plant in family V, fruit length in family I, fruit girth in family I and pericarp thickness in family IV. Both principal gene effects, additive (d) and dominance (h) gene effects were found significant for plant height and number of primary branches per plant in cross combination I; for pericarp thickness in cross combination IV; for number of fruit per plant and fruit yield per plant in cross combination V. Both additive and non-additive gene effects were found significant for most of the characters in all the interspecific cross combinations.

Keywords: Tomato, epistasis, gene effect, scaling test

Introduction
Tomato (*Solanum lycopersicum* L., 2n=2x=24) a member of nightshade family, solanaceae is one of the most important vegetable crops grown throughout the world. The red pigment in tomato (lycopene) is now being considered as the "world's most powerful natural antioxidant". It is considered as an important source of vitamin A, vitamin C and minerals. It is originated in wild form in Ecuador, Peru and Bolivia of South America which is believed to be the center of diversity of wild tomato. The tomato is a tender perennial that is almost universally cultivated as an annual. The major tomato growing countries are China, USA, Italy, Turkey, India, Egypt, Brazil, Iran and Mexico. Tomato is grown in almost all states amongst which Andhra Pradesh is the largest producer followed by Karnataka, Madhya Pradesh, Telangana, Orissa, Gujarat, Maharashtra, West Bengal, Bihar, Chhattisgarh and Himachal Pradesh. The total area under tomato in India accounts for 8.8 lakh hectares with production of 187.36 lakh tonnes. The average productivity of tomato in India is 21.20 tonnes per hectare (NHB, 2013-14) [1]. Tomato contain the carotene lycopene, one of the most powerful natural antioxidants. In some studies, lycopene, especially in cooked tomatoes, has been found to help prevent prostate cancer but other research contradicts this claim. Lycopene has also been shown to improve the skin's ability to protect against harmful UV rays. The wild taxa of tomato possess a large reserviour of economic attributes, particularly resistance to biotic and abiotic stresses and quality attributes. Interspecific crosses have been attempted to develop resistance, high quality and high yielding cultivars, to generate new variability and some cytogenetical investigations. The importance of wild taxa is apparent with the development of several resistant cultivars. In several biotic and abiotic stress areas, the survival of tomato cultivars is largely due to the presence of resistance genes in the cultivar derived from the wild species. Yield is the end product of action and interaction of number of component characters. It is difficult to combine all the desirable traits in a single variety as the major yield contributing characters have positive and/or negative association among them. Therefore, estimation of components of genetic variance is essential to formulate effective breeding program for the improvement of tomato. However, partitioning of genetic variance into its all the probable components i.e. additive, dominance and all types of epistasis with regard to individual cross is of immense value in formulating an effective and sound breeding programme.

Materials and Methods
The present investigation was carried out during 2015-16 at Distant Hybridization Farm, Dept. of Agril. Biotechnology, Anand Agricultural University, Anand. The experimental material

consisting of five families developed from six parents viz. GT 2, AT 3, EC 589496, EC 520058, WIR 5032 and ATL 10-7, each having six generations (P_1, P_2, F_1, F_2, B_1 and B_2) were evaluated in compact family block design with three replications. The suitable selfing technique for P_1, P_2 and F_1 generation and crossing technique for F_1 and backcrosses were applied. 32 days old seedlings were transplanted in the field. The individual replication was represented by five family blocks, one row each of P_1, P_2 and F_1, two rows each of B_1 and B_2 and four rows of F_2 generation. Total 10 plants were accommodated in each row. The recommended packages of agronomical practices and plant protection measures obligatory to raise healthy crop were followed both in nursery as well as in field.

Observations for total 12 different characters viz., days to flowering, plant height, number of primary branches per plant, number of fruits per plant, fruit yield per plant, average fruit weight, fruit length, fruit girth, pericarp thickness, total soluble solids, titratable acidity and lycopene content were recorded in each experimental unit i.e. generation as five plants in each P_1, P_2 and F_1, ten plants in each B_1 and B_2 and twenty plants in each F_2. An individual observation of each generation of each family was considered for statistical analysis. The mean values were used for statistical computation of all the characters studied. The data were subjected to analysis of variance for Compact Family Design described by Panse and Sukhatme [8]. The crosses showing significant differences among the progenies for the characters was subjected to generation mean analysis for the estimation of gene effects using six parameter model as suggested by Hayman [4] and Mather and Jinks [7]. The scaling test as described by Hayman and Mather [6] was used to test adequacy of additive dominance model for different characters in each cross. Joint scaling test (additive-dominance model or non-epistatic model) outlined by Cavalli [2] was also applied to generations to fit the three parameter model. In presence of non-allelic interactions various gene effects were estimated using six parameters model as suggested by Hayman [4].

Results and discussion

The individual scaling test/s and/or Y 2 value of joint scaling tests were significant with all the families for all the characters except plant height (family I), number of primary branches per plant (families I and III), number of fruits per plant (family V), fruit yield per plant (family V), fruit length (family I), fruit girth (family I) and pericarp thickness (family IV) indicating inadequacy of additive dominance model and possibility for the presence of interallelic interactions and/or linkages.

For number of days to flowering, scaling tests for all the families indicated presence of non-allelic interactions for the expression of the trait (Table 1). In all the families except family II, the principal gene effects additive as well as dominance and all the type of digenic interactions were significant, thereby suggesting importance of both additive and non-additive gene effects for the inheritance of this trait.

For plant height, the partitioning of genetic variance (Table 1) revealed that additive and dominance was involved in the expression of this trait in family I, where dominance was greater in magnitude. In family II, all the gene effects barring digenic interaction additive x dominance were highly significant, wherein dominance gene effect was greater in magnitude followed by additive x additive, additive and dominance x dominance gene effects. In families III, IV and V, additive gene effect and heterozygous interaction additive x dominance were found to be significant for this trait, epistatic effect being higher in magnitude.

The estimates of gene effects for number of primary branches per plant (Table 1) revealed that preponderance of dominance gene effect was present in family I. While, in family II all the gene effects barring digenic interaction dominance x dominance were highly significant, wherein dominance gene effect was greater in magnitude followed by additive x additive, additive x dominance and additive gene effects indicating role of both additive as well as non-additive gene actions in the expression of this trait. Additive gene effect solely involved in the expression of trait in family III. In family IV and V, fixable gene effect additive and heterozygous interaction (additive x dominance) gene effects were highly significant.

In case of number of fruits per plant (Table 1), additive and additive x dominance effects were highly significant in family I. In family II, additive, additive digenic and additive x dominance gene effects were found significant and epistasis component ('j') was having high magnitude. In family III and IV, the principal gene effects additive as well as dominance and all the type of digenic interactions were significant, thereby suggesting importance of both additive and non-additive gene effects for the inheritance of this trait. Additive and dominance gene effects were significant in family V.

The partitioning of genetic components of variation for fruit yield per plant (Table 2) indicated that in family I, all the gene effects barring dominance were found significant. In family II, dominance and additive x additive gene effects were involved for expression of this trait. In family III, principal gene effect additive, digenic interaction additive x additive and additive x dominance were significant, thereby suggesting importance of both additive as well as non-additive gene effects for the inheritance of character. In family IV, additive and heterozygous interaction (additive x dominance) gene effects were highly significant. Additive and dominance gene effects were significant in family V. The present findings are similar to the results of Zdravkovic *et al*. (2011) [11], Dutta *et al*. (2013) [3], Kumar *et al*. (2013) [6], Shalaby (2013) [9] and Singh *et al*. (2014) [10] who reported significance of both additive and non-additive gene actions both.

For average fruit weight, all the gene effects were found highly significant (Table 2) except additive x additive in family I and II. Additive, additive x additive and additive x dominance gene effects were highly significant in family III. In family IV, principal gene effects additive, dominance epistatic additive x dominance and dominance x dominance were involved for expression of this trait.

The estimates of gene effects for fruit length (Table 2) in family I revealed additive gene effect was highly significant. In family II, additive, dominance and digenic interaction dominance x dominance were significant. In family III, all gene effects except additive x additive were significant. In case of family IV, all the gene effects barring additive x dominance were found significant. Additive and additive x additive gene effects were found significant in family V. The opposite signs of dominance and dominance x dominance gene effects indicated presence of duplicate epistasis in nature in the inheritance of this trait in families II, III and IV.

For fruit girth, the partitioning of genetic variance (Table 2) revealed that only additive gene effect was observed to be significant with both the approaches in the expression of this trait in family I. In family II, additive and additive x dominance gene effect governed the expression of this trait.

Additive, dominance and additive x dominance were found to be significant in family III. In family IV, individual scaling test 'B' and in family V, Scaling tests 'B' and 'C' were significant, which suggested inadequacy of dominance model.

In case of pericarp thickness (Table 3), all the gene effects except additive x dominance were found to be highly significant, which led to predominance of non-additive gene effect in family I. All gene effects were found highly significant in family II. Additive and additive x additive gene effects were highly significant in family III. In family IV, additive and dominance gene effects were highly significant, where additive gene effect was higher in magnitude. In family V, scaling tests 'B' and 'C' were significant, which suggested inadequacy of dominance model.

The estimates of gene effects for total soluble solids (Table 3) revealed that additive, additive x additive and heterozygous interaction (additive x dominance) were found highly significant in family I for this trait. In family II, additive, additive x dominance and dominance x dominance gene effects were highly significant. In family III and IV, all the gene effects were found significant barring dominance x dominance and digenic interaction additive x additive, respectively. Additive, dominance and additive x additive gene effects were found highly significant in family V.

For titratable acidity (Table 3), in family I, all the gene effects except additive x additive were found significant. All the gene effects were found highly significant in family II. In Family III and IV, additive and dominance x dominance gene effects were found significant, where additive gene effect was higher in magnitude. In family V, additive, dominance and dominance x dominance were found highly significant, in which both the principal gene effects were greater in magnitude.

In case of lycopene content (Table 3), in family I, all the gene effects were found highly significant except heterozygous interaction. In family II, scaling tests 'A' and 'C' were significant, which suggested inadequacy of dominance model. However, only additive component of six parameters model was highly significant, thereby suggesting additivity of genes, but higher order interaction, probably pseudo additive gene action could be present. In family III and V, additive, additive x dominance and dominance x dominance were found significant. Additive and dominance x dominance gene effects were found highly significant in family IV.

Table 1: Estimates of Simple Scaling Test and gene effects for days to flowering, plant height, number of primary branches per plant and number of fruits per plant in five crosses of tomato.

Crosses	Gene effect													
	Scaling Tests				Three parameters model			X^2 at 3 d.f.	Six parameters models					
	A	B	C	D	m	$\hat{d}$	$\hat{h}$		m	$\hat{d}$	$\hat{h}$	$\hat{i}$	$\hat{j}$	$\hat{l}$
Days to flowering														
I	1.53	-9.67**	-2.87	2.63**	-	-	-	85.92**	39.80**	1.20**	-23.80**	-5.27**	11.20**	13.40**
II	-1.07	4.87**	6.33**	1.27	-	-	-	41.37**	35.60**	0.87**	-6.13	-2.53	-5.93**	-1.27
III	3.33**	-1.47	12.80**	5.47**	-	-	-	57.53**	43.23**	1.77**	-25.90**	-10.93**	4.80**	9.07**
IV	-5.40**	4.13**	4.73*	3.00**	-	-	-	69.84**	38.23**	1.63**	-18.77**	-6.00**	-9.53**	7.27*
V	-6.47**	-3.27**	-4.27	2.73*	-	-	-	40.76**	38.50**	4.23**	-23.43**	-5.47*	-3.20**	15.20**
Plant height														
I	-2.73	-27.67	-36.27	-2.93	100.44**	-34.92**	38.40**	2.90	-	-	-	-	-	-
II	20.13	-12.73	-116.87**	-62.13**	-	-	-	56.33**	-21.47	-28.87**	266.14**	124.27**	32.87	-131.67**
III	-9.33	-51.53**	-57.47	1.70	-	-	-	10.06*	115.27**	-48.33**	-52.00	-3.40	42.20*	64.27
IV	-17.00	-63.20**	-84.80**	-2.30	-	-	-	17.54**	107.56**	-40.17**	-55.96	4.60	46.20*	75.60
V	36.07*	-28.13	2.80	-2.57	-	-	-	9.20*	114.76**	-57.30**	10.17	5.13	64.20**	-13.07
Number of primary branches per plant														
I	-0.13	1.87	-2.00	-1.87	8.99**	-3.88**	4.00**	2.25	-	-	-	-	-	-
II	1.00	-5.93**	-18.07**	-6.57**	-	-	-	109.39**	-2.87	-4.13**	23.40**	13.13**	6.93**	-8.20
III	0.87	-1.47	-0.80	-0.10	9.81**	-4.81**	-1.01	2.43	-	-	-	-	-	-
IV	-0.53	-8.67**	-11.67**	-1.23	-	-	-	73.82**	8.33**	-5.13**	-2.00	2.47	8.13**	6.73
V	1.73	-3.80**	0.33	1.20	-	-	-	11.29*	14.37**	-6.10**	-7.90	-2.40	5.53**	4.47
Number of fruits per plant														
I	-259.53**	75.53	-62.60	60.70	-	-	-	75.91**	343.64**	-207.60**	-234.64	-121.31	-335.10**	305.25
II	-113.07*	-376.93**	-686.40*	-98.20*	-	-	-	107.56**	139.21	-317.10**	-81.51	196.28*	263.90**	293.86
III	-158.93**	425.40*	-713.20**	-489.83**	-	-	-	56.68**	-645.73**	-318.24**	2200.60**	979.10**	-583.79**	-1245.04**
IV	-289.47**	350.20**	-650.60**	-355.67**	-	-	-	95.00**	-440.30**	-255.58**	1559.68**	710.82**	-639.48**	-771.40**
V	132.13	-50.47	-72.80	-77.23	431.36**	-413.96**	-158.31**	1.26	-	-	-	-	-	-

Table 2: Estimates of Simple scaling test and gene effects for fruit yield per plant, average fruit weight, fruit length and fruit girth in five crosses of tomato.

Crosses	Gene effect													
	Scaling Tests				Three parameters model			X^2 at 3 d.f.	Six parameters models					
	A	B	C	D	m	$\hat{d}$	$\hat{h}$		m	$\hat{d}$	$\hat{h}$	$\hat{i}$	$\hat{j}$	$\hat{l}$
Fruit yield per plant														
I	-0.77**	-0.06	0.46	0.64**	-	-	-	18.00**	1.72**	-0.11**	-2.06	-1.29**	-0.71*	2.11**
II	-0.24	0.02	-1.73**	-0.76**	-	-	-	38.45**	-0.89**	-0.20	3.21**	1.52**	-0.26	-1.30
III	-1.09**	0.53*	-1.19**	-0.32*	-	-	-	63.50**	-0.07	-0.15**	1.45	0.63*	-1.62**	-0.08
IV	-1.10**	0.31	-1.44*	-0.32	-	-	-	49.04**	-0.17	-0.15**	1.36	0.65	-1.41**	0.14
V	-0.04	0.17	-0.38	-0.26	0.57**	-0.22**	0.52**	3.39	-	-	-	-	-	-
Average fruit weight														
I	-9.52**	-0.77*	-10.32**	-0.02	-	-	-	65.86**	9.90**	8.69**	-16.93**	0.03	-8.75**	10.25**
II	-12.35**	0.31	-10.03**	1.01	-	-	-	113.56**	11.68**	8.68**	-21.86**	-2.01	-12.66**	14.06**
III	-9.91**	-0.76	-16.27**	-2.81**	-	-	-	99.47**	4.64**	9.41**	-6.74	5.61**	-9.15**	5.05
IV	-5.58**	-2.02**	-10.15**	-1.28	-	-	-	77.99**	7.34**	8.92**	-7.99*	2.56	-3.55**	5.04*
V	-10.44**	-0.47	-16.69**	-2.89**	-	-	-	387.76**	4.55**	9.41**	-6.48	5.78**	-9.97**	5.12*
Fruit length														
I	-0.23	0.11	0.09	0.10	2.17**	0.95**	0.05	2.61	-	-	-	-	-	-
II	-1.09**	0.35**	-0.41	0.17	-	-	-	32.14**	2.83**	1.14**	-1.69*	-0.33	-1.44	1.07*
III	-0.91**	-0.10	-0.43	0.29*	-	-	-	13.50**	3.04**	1.05**	-2.62**	-0.59	-0.81**	1.60**
IV	-0.17	-0.31**	0.12	0.30*	-	-	-	18.37**	2.81**	0.86**	-1.57*	-0.60*	0.14	1.09*
V	0.19	-0.35*	-0.85**	-0.35	-	-	-	25.20**	1.50**	0.93**	1.19	0.69*	0.54	-0.54
Fruit girth														
I	-0.02	0.18	0.59*	0.21	2.15**	0.89**	0.02	6.24	2.57**	0.89**	-0.72	-0.43	-0.19	0.27
II	-0.52*	0.47**	0.31	0.18	-	-	-	22.17**	2.70**	0.99**	-0.86	-0.36	-0.99**	0.40
III	-0.73**	-0.03	-0.50*	0.13	-	-	-	10.47*	2.62**	0.98**	-1.64*	-0.26	-0.69**	0.10
IV	-0.03	-0.37**	0.26	0.33	-	-	-	28.51**	2.86**	0.88**	-1.45	-0.66	0.35	1.06
V	0.16	-0.19*	-0.58**	-0.28	-	-	-	10.77*	1.57**	0.87**	1.21	0.56	0.35	-0.53

Table 3: Estimates of simple scaling tests and gene effects for pericarp thickness, total soluble solids, titratable acidity and lycopene content in five crosses of tomato.

Crosses	Gene effect													
	Scaling Tests				Three parameters model			X^2 at 3 d.f.	Six parameters models					
	A	B	C	D	m	$\hat{d}$	$\hat{h}$		m	$\hat{d}$	$\hat{h}$	$\hat{i}$	$\hat{j}$	$\hat{l}$
Pericarp thickness														
I	-0.84*	-0.33	0.84	1.01**	-	-	-	17.64**	4.30**	1.16**	-5.60**	-2.01**	-0.50	3.18**
II	-3.00**	0.09	-1.08**	0.91**	-	-	-	210.48**	4.23**	1.15**	-6.68**	-1.83**	-3.09**	4.73**
III	-0.67	-0.14	-2.17**	-0.68**	-	-	-	41.57**	1.50**	1.53**	0.89	1.36**	-0.53	-0.56
IV	0.47	-0.18	-0.16	-0.23	2.87**	1.56**	-0.87**	3.36	-	-	-	-	-	-
V	0.02	-0.35*	-1.15**	-0.41	-	-	-	16.21**	1.57**	1.01**	0.97	0.82	0.38	-0.49
Total soluble solids														
I	-0.10	-1.45**	-2.55**	-0.50**	-	-	-	98.08**	4.27**	-0.97**	0.63	1.00**	1.35**	0.55
II	-0.60*	-2.35**	-3.60**	-0.33	-	-	-	115.00**	4.62**	-1.32**	-1.97	0.65	1.75**	2.30**
III	0.60*	-1.65**	-3.30**	-1.13*	-	-	-	40.20**	2.78**	-1.08**	4.17*	2.25*	2.25**	-1.20
IV	-0.95**	-2.30**	-2.65**	0.30	-	-	-	56.00**	5.80**	-0.90**	-3.75*	-0.60	1.35**	3.85**
V	-0.55	-1.55**	-5.30**	-1.60**	-	-	-	77.54**	2.35**	-1.25**	5.85**	3.20**	1.00	-1.10
Titratable acidity														
I	4.27**	-0.97**	0.63	1.00**	-	-	-	14.06**	0.29	-0.17**	3.01*	0.34	-0.66*	-2.77**
II	4.62**	-1.32**	-1.97	0.65	-	-	-	290.06**	-0.19	-0.11**	3.87**	0.69**	-0.66**	-3.14**
III	2.78**	-1.08**	4.17*	2.25*	-	-	-	260.17**	1.12**	-0.13**	1.54	-0.52	-0.34	-2.19**
IV	5.80**	-0.90**	-3.75*	-0.60	-	-	-	168.91**	1.44**	-0.13**	0.62	-0.84	-0.32	-1.63*
V	2.35**	-1.25**	5.85**	3.20**	-	-	-	143.86**	-0.06	-0.08**	4.41**	0.60	-0.50	-3.66**
Lycopene content														
I	0.09	-0.30	-2.93**	-1.36**	-	-	-	75.66**	3.73**	-1.33**	5.63**	2.71**	0.38	-2.50**
II	-1.14**	-0.12	-1.57*	-0.16	-	-	-	15.58**	4.20**	-0.15**	0.46	0.31	-1.02	0.95
III	-1.89**	-1.11**	-3.37**	-0.18	-	-	-	311.48**	5.70**	-0.68**	-1.16	0.37	-0.78**	2.63**
IV	-1.62**	-1.11**	-3.10**	-0.18	-	-	-	76.66**	5.57**	-0.82**	-0.76	0.36	-0.51	2.36**
V	-1.31**	-0.63**	-2.10**	-0.08	-	-	-	44.70**	5.37**	-0.42**	-0.18	0.17	-0.68*	1.77*

Conclusion

The system of breeding that can be employed for improvement of character depends upon the type of gene action involved for its expression. The type and magnitude of gene effects differed for different characters in the same cross and for the same character in different crosses, which necessitates specific handling of individual cross in segregating generations, and it would be advantageous for improvement of characters under study. In general, the character governed or preponded by fixable additive gene effect could be improved through pedigree selection method. Majority of the characters were controlled by non-additive

gene effect or additive and non-additive gene effects in different crosses hence, those could be successfully improved by heterosis breeding or hybridization followed by cyclic method of breeding i.e., recurrent selection.

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